

Distribution of *Alternaria* species among sections. 3. Sections *Infectoriae* and *Pseudoalternaria*

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ABSTRACT—Morphological examination of material conforming to the morphological description of *Alternaria* sect. *Infectoriae* (but not phylogenetically characterized) allowed the inclusion of nine additional species in this section, which thus encompasses 34 species. *Alternaria* sect. *Pseudoalternaria* consists of two species and one misidentified isolate that represents a novel taxon, described here as *Alternaria parvicaespitosa*. Emended descriptions of A. sect. *Infectoriae* and A. sect. *Pseudoalternaria* are presented, and their species are listed.

KEY WORDS—*Alternaria infectoria*, *Alternaria rosae*, *Lewia*

This article is dedicated to the jubilee of the flourishing 200-year-old girl, *Alternaria*.

Introduction

Alternaria Nees 1816 is a large pleomorphic genus that comprises approximately 280 distinguishable species (Simmons 2007). A large series of morphological and phylogenetic studies have attempted to better resolve the phylogeny of *Alternaria* and other alternarioid hyphomycetes by utilizing more than ten different genomic loci (Pryor & Bigelow 2003; Hong et al. 2005; Runa et al. 2009; Lawrence et al. 2012, 2013, 2014; Woudenberg et al. 2013, 2014; Armitage et al. 2015). Several well-supported lineages (phylogenetic species-groups) have been revealed within the alternarioid hyphomycetes and have led to several taxonomic novelties. The genus *Alternaria* was recently divided into eight taxonomic sections by Lawrence et al. (2013) followed by the elevation

of 19 additional clades by Woudenberg et al. (2013, 2014), Grum-Grzhimaylo et al. (2016), and Lawrence et al. (2016), thereby bringing the total number of sections of *Alternaria* to 27.

All works support the monophyly of two morphologically peculiar *Alternaria* groups, two of several groups having members with catenate, small-spored conidia. Recently these groups were elevated to sectional status, as *A. sect. Infectoriae* and *A. sect. Pseudoalternaria*.

Twenty-five species were indicated as members of sect. *Infectoriae* by Lawrence et al. (2013). Woudenberg et al. (2013) added two additional species to this clade, bringing the total number of recognized species to 27. Lawrence et al. (2013) also mentioned three species (*A. peglionii*, *A. dianthicola*, and *A. photistica*) that cannot be included in sect. *Infectoriae*. The sequenced strain of *A. peglionii* (CBS 103.26) was not the type, and this species was previously listed as *incertae sedis* (Simmons 2007). The sequenced strain of *A. dianthicola* was not designated by E.G. Simmons as a representative strain. When a representative strain of *A. dianthicola* was utilized it clustered distantly to sect. *Infectoriae* (Woudenberg et al. 2013). Also Lawrence et al. (2013) and Woudenberg et al. (2013) used the same strain of *A. photistica* (EGS 35.172), but it was obtained from different sources. Conclusions by Woudenberg et al. (2013) based on molecular and morphological data placed *A. photistica* in sect. *Panax* and *A. dianthicola* in sect. *Dianthicola*. Ariyawansa et al. (2015) described a new species, *A. murispora*, in section *Infectoriae* based on ascomatal morphology and DNA analysis; no living culture or conidial state of this species is known. Ariyawansa et al. (2015) also noted that the type isolate of *Xenobotryosphaeria calamagrostidis* (CBS 303.71) clustered in sect. *Infectoriae* (albeit with low support) and only the sexual state was produced in culture and clearly differed from species within *Alternaria* sect. *Infectoriae*. The authenticity of *X. calamagrostidis* remains unresolved and would benefit from a re-examination of morphological and molecular characters for this peculiar isolate/taxon.

The number of species recovered by phylogenetic species recognition approaches can differ from that revealed by morphological analysis. Very likely a morphological concept favors splitting. For instance, phylogenetic analyses of three genomic regions from 39 infectoria species-group isolates (Andersen et al. 2009) were unable to provide strong support for species-level designations for most isolates. No correlations were found among phylogenetic data, metabolite production, morphological identity, proascoma formation, ability to grow at 37°C, and host or geographic origin. Gannibal & Yli-Mattila (2007), who utilized a set of 52 infectoria species-group isolates (including representative strains of eight morphospecies), were unable to divide the isolates into distinct groups based on data from molecular fingerprinting.

The main discriminating morphological features of many *Alternaria* sect. *Infectoriae* species are small conidia (in culture usually no longer than 60 µm) and long secondary conidiophores (Lawrence et al. 2013; Woudenberg et al. 2013). Ten species have a known sexual state (*A. alternarina*, *A. daucicaulis*, *A. ethzedia*, *A. hordeiaustralica*, *A. hordeicola*, *A. infectoria*, *A. intercepta*, *A. murispora*, *A. scrophulariae*, and *A. viburni*). Some strains are capable of producing proascoma in axenic culture, suggesting that members of this group, at least in part, are homothallic (Andersen et al. 2009). In general fungi in this section are common. Usually they exist as saprobes showing no substrate preference. This group produces reliable chemotaxonomic markers (Christensen et al. 2005; Andersen et al. 2002, 2009). Some authors have shown that strains of this group do not produce mycotoxins generally made by other small-spored *Alternaria* sections (e.g., sect. *Alternaria*) (Andersen et al. 2002). Other studies revealed the ability of some species to produce alternariol and monomethyl ether (Oviedo et al. 2013), which probably is common for other *Alternaria* sections.

Lawrence et al. (2014) assigned two species, sister to *A.* sect. *Infectoriae*, to a new genus, “*Pseudoalternaria*” nom. inval. This placement became untenable after all alternarioid hyphomycetes were collected under the single generic name *Alternaria* (Woudenberg et al. 2013). The thorough review by Lawrence et al. (2016) resurrected “*Pseudoalternaria*” as a new section, *Alternaria* sect. *Pseudoalternaria*, typified by a new species, *Alternaria arrhenatheri*.

Section *Pseudoalternaria* currently consists of two described species, *A. arrhenatheri* D.P. Lawr. et al. and *A. rosae* E.G. Simmons & C.F. Hill, and one misidentified isolate (X1272, isolated from blueberry and identified as *A. rosae* by Zhu & Xiao 2015) but which represents a third/new species (based on molecular and morphological data), described here as *A. parvicaespitosa*.

Ongoing molecular studies will likely identify additional species and novel lineages within *Alternaria*. However, living cultures are not known for several morphospecies. Additionally some herbaria materials are recalcitrant to DNA isolation and/or devoid of conidia. Fortunately, the morphological diversity of *Alternaria* has been well studied (Simmons 2007). Classical comparative morphological studies are useful for establishing phylogenetic affiliation. This work is a continuation of the series started with the manuscripts on sections *Porri* and *Alternaria* (Gannibal 2015, 2016). The aim of the present work is to detect among phylogenetically unexamined *Alternaria* species those species that fit the current morphological circumscription of sections *Infectoriae* and *Pseudoalternaria* and to emend the morphological concept of these sections.

Materials & methods

The morphology of almost all *Alternaria* species with legitimate names was analyzed with regard to conformity with criteria of *Alternaria* sections *Infectoriae* and *Pseudoalternaria*. The morphological assessment was based on descriptions made by Simmons (2007) or using original diagnoses and illustrations for species described after 2007. Descriptions of three species included in sect. *Infectoriae* were found in Roberts (2008: *A. roseogrisea*), Roberts et al. (2010: *A. cerasidanica*), and Ariyawansa et al. (2015: *A. murispora*). Strain X1272 was cultured on potato carrot agar (PCA) at 24°C under light/dark cycle (12/12 h) for 7–10 days to promote sporulation in order to describe this as a new taxon; the holotype specimen (a metabolically inactive dried PCA culture) was conserved in the Mycological Herbarium, All-Russian Institute of Plant Protection, Saint Petersburg, Russia (LEP).

Results & discussion

The evaluation of all available descriptions of *Alternaria* species allowed for the inclusion of nine additional species in sect. *Infectoriae*, two of which have no known living isolates. The diversity of this section consists of 34 morphologically recognizable species. Recircumscription of the misidentified isolate, *A. rosae* strain X1272 (Zhu & Xiao 2015), allowed for the addition of one species to sect. *Pseudoalternaria* bringing the total number of species in this clade to three.

Alternaria parvicaespitosa Gannibal & D.P. Lawr., sp. nov.

FIGS 1, 2

MYCOBANK MB 816666

Differs from *Alternaria rosae* by its shorter conidial chains (non-branched parts) and narrower conidia with fewer transverse septa.

TYPE: USA, California, Tulare, harvested blueberry fruit from a commercial fruit-packing center, 6 June 2013, X.Q. Zhu & C.L. Xiao X1272 (Holotype, LEP 014858, a metabolically inactive dried culture).

ETYMOLOGY: *parvi* (Latin), small; *caespitosa* (Latin), bushy.

Sporulation on PCA occurs primarily in discrete bushy clumps. Conidiophores arise as series in close proximity to one another from submerged or (more often) aerial hyphae. Aerial conidiogenous hyphae are hyaline filiform or thick colored conidiophore-like and may be positioned vertically or horizontally. Most conidiophores remain relatively short, $35\text{--}70 \times 3\text{--}4\ \mu\text{m}$. They are simple or sometimes produce two branches. Each branch is multigeniculate (1–6 genua near conidiogenous loci). The conidiogenous sites produce short chains of conidia ($\leq 3\text{--}4$ between branching points) which usually have one or a few branches due to the production of several conidiogenous sites on an apical secondary conidiophore or (very rarely) due to the formation of a lateral secondary conidiophore. Aged clumps of conidia developed on a single conidiophore may comprise ≤ 20 conidia.

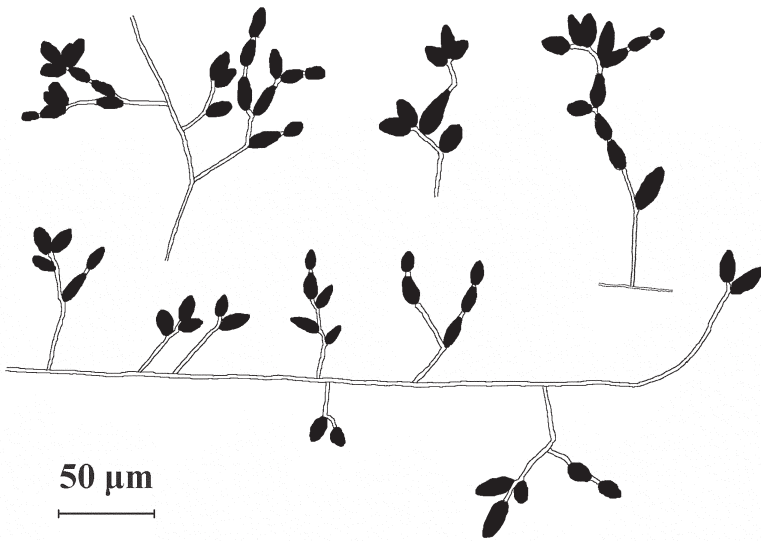


FIG. 1. *Alternaria parvicaespitosa* (ex holotype, LEP 014858): sporulation pattern.

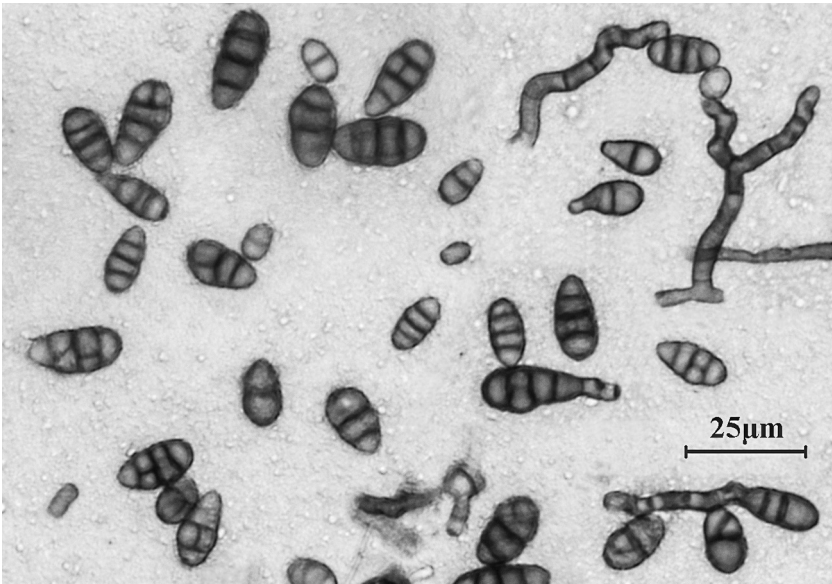


FIG. 2. *Alternaria parvicaespitosa* (ex holotype, LEP 014858): conidia and conidiophores.

Both juvenile and mature conidia are ovoid or elliptical. Small portion of conidia is obclavate. Maximum size range of mature conidia is $10\text{--}25 \times 7\text{--}12\ \mu\text{m}$. Conidia have 1–3(–4) transverse septa and at most one longiseptum in 1–2 of the transverse segments. Rarely conidia have no longisepta. Most conidia have no secondary conidiophores; but any conidium, including 1-celled units and conidia with relatively large conidial bodies, can produce an apical secondary conidiophore (a single cell ca $3 \times 3\ \mu\text{m}$) or a geniculate extension $5\text{--}28\ \mu\text{m}$ long with 2–5 conidiogenous sites. Rarely apical secondary conidiophores are branched. Lateral secondary conidiophores appear rarely and when present are short. Conidia and conidiophores are concolorous, medium brown. The conidium outer wall is smooth or (in the largest conidia) slightly punctulate.

Alternaria species in sections *Infectoriae* and *Pseudoalternaria* are listed in TABLE 1.

Herein we present emended and somewhat expanded versions of the descriptions of *Alternaria* sect. *Infectoriae* by Woudenberg et al. (2013) and of *A.* sect. *Pseudoalternaria* by Lawrence et al. (2016). Characters are quantified when appropriate, and examples are provided of species whose quantified characters either depart from the section norm or conform to it.

Alternaria* sect. *Infectoriae Woudenb. & Crous, Stud. Mycol. 75: 194. 2013; emend. Gannibal & Lawrence

On PCA or weak potato dextrose agar (WPDA) primary conidiophores arise from the agar surface or from vegetative aerial hyphae. Primary conidiophores are solitary or aggregated, cylindrically straight or geniculate, simple or branched, short to long, septate, brown, $20\text{--}150 \times 3\text{--}4\ \mu\text{m}$, with one or several (2–6) conidiogenous loci (pores) at the apex and throughout its length. Conidial chains are moderately long to long, simple or (usually) branched. Branching is produced by the occurrence of several conidiogenous loci on apical secondary conidiophores or (rarely: in some species completely absent) lateral secondary conidiophores.

Young conidia are ovoid, broadly ovoid, ellipsoid or subellipsoid, erostrate or with short to long secondary conidiophore at the apex. Mature conidia are obclavate, ovoid, ellipsoid or subellipsoid; small or moderate in size; with (1–)4–7(–10) transverse and no, one or a few longitudinal septa; slightly constricted near some transverse septa. Size of conidia is $30\text{--}60 \times 6\text{--}15\ \mu\text{m}$ (except conidia with long secondary conidiophores); sometimes a large number of conidia remain small ($12\text{--}30 \times 5\text{--}10\ \mu\text{m}$). Several species (e.g., *A. triticina*) can produce relatively larger conidia, $\leq 60 \times 25\ \mu\text{m}$, not including secondary

TABLE 1. List of *Alternaria* spp. assigned to *A. sect. Infectoriae* and *A. sect. Pseudoalternaria*.

Names with bracketed annotations = species with phylogenetic data (in the cited references).

Unannotated names = species with reliable living cultures and herbarium specimens.

Names with asterisk = species for which no known living isolates are available.

Section *Infectoriae*

- A. alternarina* E.G. Simmons (Lawrence et al. 2013, 2014)
- A. arbusi* E.G. Simmons (Lawrence et al. 2013, 2014)
- A. astragali* Wangeline & E.G. Simmons
- A. caespitosa* (de Hoog & C. Rubio) Woudenb. & Crous (Woudenberg et al. 2013; Grum-Grzhimaylo et al. 2015)
- A. californica* E.G. Simmons & S.T. Koike (Lawrence et al. 2013, 2014)
- A. cerasi* Potebnia [*]
- A. cerasidanica* R.G. Roberts
- A. daucicaulis* E.G. Simmons (Lawrence et al. 2013, 2014)
- A. ethzedia* E.G. Simmons (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013; Grum-Grzhimaylo et al. 2015)
- A. frumenti* E.G. Simmons & C.F. Hill (Lawrence et al. 2013, 2014)
- A. geophila* Dasz.
- A. graminicola* E.G. Simmons (Lawrence et al. 2013, 2014)
- A. hordeiaustralica* E.G. Simmons & Alcorn (Lawrence et al. 2013, 2014)
- A. hordeicola* E.G. Simmons & Kosiak (Lawrence et al. 2013, 2014)
- A. humuli* E.G. Simmons (Lawrence et al. 2013, 2014)
- A. incomplexa* E.G. Simmons (Lawrence et al. 2013, 2014)
- A. infectoria* E.G. Simmons (Pryor & Bigelow 2003; Lawrence et al. 2013; Woudenberg et al. 2013; Grum-Grzhimaylo et al. 2015)
- A. intercepta* E.G. Simmons (Lawrence et al. 2013, 2014)
- A. iridiaustralis* E.G. Simmons, Alcorn & C.F. Hill
- A. litorea* (Pivkin & Zvereva) E.G. Simmons [*]
- A. merytae* E.G. Simmons (Lawrence et al. 2013, 2014)
- A. metachromatica* E.G. Simmons (Hong et al. 2005; Lawrence et al. 2013, 2014)
- A. murispora* Ariyaw. & K.D. Hyde [*] (Ariyawansa et al. 2015)
- A. novae-zelandiae* E.G. Simmons (Lawrence et al. 2013, 2014)
- A. oregonensis* E.G. Simmons (Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013; Grum-Grzhimaylo et al. 2015)
- A. roseogrisea* R.G. Roberts
- A. scrophulariae* (Desm.) Rossman & W.C. Allen (Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013; Grum-Grzhimaylo et al. 2015)
- A. seleniiphila* Wangeline & E.G. Simmons
- A. slovacica* (Svob.-Pol., L. Chmel & Bojan.) Woudenb. & Crous (Woudenberg et al. 2013; Grum-Grzhimaylo et al. 2015)
- A. triticimaculans* E.G. Simmons & Perelló (Lawrence et al. 2013, 2014)
- A. triticina* Prasada & Prabhu (Pryor & Bigelow 2003; Lawrence et al. 2013)
- A. vaccinii* E.G. Simmons
- A. ventricosa* R.G. Roberts (Lawrence et al. 2013, 2014)
- A. viburni* E.G. Simmons (Lawrence et al. 2013, 2014)

Section *Pseudoalternaria*

- A. arrhenatheri* D.P. Lawr., Rotondo & Gannibal (Lawrence et al. 2014, 2016)
- A. rosae* E.G. Simmons & C.F. Hill (Lawrence et al. 2013, 2014)
- A. parviccaespitosa* Gannibal & D.P. Lawr. (Zhu & Xiao 2015, as "*A. rosae*")

conidiophores. Some mature conidia remain erostrate or produce secondary conidiophores. Apical secondary conidiophores are short or long, simple or branched, usually geniculate with one or (often) a few ($\leq 5-7$) conidiogenous loci over its entire length. Approximately 30% of mature conidia produce at least 4 transverse septa in the conidium body terminating in a chain that is ovoid or ellipsoid and has no secondary conidiophores, beak or conidiogenous loci on apical cell. At least 10% of mature conidia produce apical secondary conidiophores that are longer than conidial body and exceed 30 μm (often reaching 50–100+ μm). Long apical conidiophores having only one transverse septum and no longitudinal septa are sometimes produced by very small conidia. Some conidia have short solitary lateral secondary conidiophores with one or two conidiogenous loci. Conidia are pale brown, yellowish to dark brown; the spore wall is smooth or conspicuously ornamented.

Ascomata on natural substrata are erumpent, almost superficial or submerged into host cortex, scattered, subglobose to sphaeroid with a short blunt beak, dark, smooth, thin-walled at maturity. Asci subcylindrical, straight, curved or muriform, usually 8-spored. Mature ascospores are ellipsoid, 5–7 transverse septa, forming one or two longitudinal septa through each central or sometimes through apical transverse segments, conspicuously constricted at median septum and slightly so at two other transepta, brown.

Colony color on rich media like PDA, PSA, DRYES or Czapek-Dox agar, is light: white, delicate rose, light gray or pale olivaceous. Colonies usually do not sporulate in the dark, especially on rich media. Sporulation is usually copious on PCA or V8 agar medium, intensive light or near UV light (when grown in glass Petri dishes).

Alternaria* sect. *Pseudoalternaria D.P. Lawr., Rotondo & Gannibal, Mycol. Progr.

15:3 [11 of 22]. 2016; emend. Gannibal & Lawrence

On PCA or WPDA sporulation aggregated, appearing granular to the naked eye. Mycelium subhyaline to light brown; hyphae smooth, branched, septate, 3.8–5 μm wide. Primary conidiophores aggregated on agar surface or developing from arachnoid aerial hyphae, simple or branched, septate, smooth, medium brown, 8.7–37.5 $\times$ 3.7–5 μm ($M = 18.1 \times 4.8 \mu\text{m}$), simple with single apical pore. Secondary conidiophores short to long, simple to multi-geniculate with one to many conidiogenous loci. Conidia 10–32.5 $\times$ 4.7–10 μm ($M = 16.8 \times 7.3 \mu\text{m}$), mostly catenulate, ellipsoid to obclavate, medium brown to golden brown, 3–4 transverse septa, 1–2 longitudinal septa, smooth, may produce a secondary conidiophore (false beak).

Acknowledgments

The authors are grateful to Dr. Hiran Ariyawansa (Guizhou Academy of Agricultural Sciences, Guizhou University, Guiyang, China) and Dr. Andrew Armitage (Genetics and Crop Improvement, East Mailing Research, UK) for presubmission review. This work was supported by Russian Science Foundation (project #14-26-00067).

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